

Congener comparison of native (*Zostera marina*) and introduced (*Z. japonica*) eelgrass at multiple scales within a Pacific Northwest estuary

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Abstract A congener comparison of native (*Zostera marina*) and introduced (*Zostera japonica*) eelgrasses was conducted in Willapa Bay, Washington, USA. Along intertidal transects, *Z. japonica* (0.1–1.5 m above mean lower low water [MLLW]) occurred above *Z. marina* (<0.6 m MLLW). Both species declined in shoot length at higher elevation, but *Z. japonica* was always shorter (20 vs. 100 cm) and occurred at higher shoot density (>3,800 vs. <360 m⁻² in *Z. marina*). *Z. japonica* exhibited greater seasonal variation in biomass, with increases supported by both sustained asexual reproduction (rhizome branching) and recruitment from seeds (30 vs. <5% in *Z. marina*). *Z. japonica*'s successful invasion appears related to small size and high reproductive output, allowing it to

spread quickly in a variable and stressful intertidal environment where competitive effects are low. Based on interannual changes in abundance, the native eelgrass has also recently increased in Willapa Bay, and one hypothesis involves “engineering” of suitable habitat at higher tidal elevations by *Z. japonica*.

Keywords Seagrasses · Invasion · Life history · Estuary · Congener · Tidal elevation · *Zostera marina* · *Zostera japonica* · Willapa Bay · Washington · Darwin's naturalization hypothesis

Introduction

Congener comparison is a powerful method to determine attributes of introduced species that may make them invasive (Mack 1996). The analysis involves choosing two closely-related species that co-occur, one of which is invasive and the other rare and/or stable in population size. Then, the two species are compared across their life cycle to determine traits that contribute to the difference in performance. In some cases, these comparisons emphasize autecological traits. For instance, invasive species of *Pinus* in South Africa have more prolific reproduction and shorter juvenile periods than species that have been introduced but have not become invasive (Rejmanek and Richardson 1996). More

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recently, congener comparisons have addressed differences in species interactions that could contribute to invasion success (Mitchell et al. 2006). Successful invaders may be those that can outcompete native congeners or escape natural enemies that kept them in check in their native range (Maron and Vila 2001; Vila and Weiner 2004), or, alternatively, the presence of a closely-related species may impair invasion (Daehler 2001).

In this paper, we compare the life histories of an introduced eelgrass (*Zostera japonica* Aschers. & Graebn.) and native congener (*Z. marina* L.) that co-occur on tideflats in Willapa Bay, Washington. Although *Z. marina* and *Z. japonica* have been studied concurrently in other locations, both where *Z. japonica* is native (Lee et al. 2006) and where it is introduced (Harrison 1982a; Thom 1990; Nomme and Harrison 1991a, b; Hahn 2003; Bando 2006; Shafer et al. 2007), their life histories have not previously been compared to test hypotheses in invasion biology.

Two species of *Zostera* are the only angiosperms present below salt marshes in Pacific Northwest estuaries, barring sporadic occurrence of *Ruppia maritima* (Harrison 1982b; Kaldy 2006; personal observation). *Z. marina* is a circumglobal eelgrass that can form monospecific stands in shallow coastal water (Green and Short 2003; Moore and Short 2006). It is declining in many locales due primarily to onshore activities that reduce water clarity (Lotze et al. 2006; Moore and Short 2006; Orth et al. 2006a). *Z. japonica* appeared in Washington state by 1957 (Harrison and Bigley 1982). It may have been introduced from Japan with Pacific oysters (*Crassostrea gigas*) (Wonham and Carlton 2005), which were transported annually from the 1920 s to 1977 for aquaculture (White et al. 2009). Thus a likely geographic origin is Miyagi prefecture, Japan (38°N), but no genetic analysis exists to test this hypothesis. In the northeast Pacific, *Z. japonica* is invasive, transforming tideflats that are naturally unvegetated above the elevation of *Z. marina* (Harrison 1982a; Thom 1990; Hahn 2003; Kaldy 2006). It occurs widely along the west coast from British Columbia (49.5°N) to southern Oregon (43.1°N; Larned 2003), with further spread being controlled in northern California (40.8°N; Schlosser et al. 2005, cited in Kaldy 2006). This successful invasion has occurred despite a decline in *Z. japonica* in parts of

its native range on western Pacific shores (Lee 1997). This native range, from Viet Nam to northern Russia, includes tropical and sub-tropical latitudes even though *Z. japonica* is generally considered a temperate seagrass (Lee 1997; Shin and Choi 1998).

Seagrasses show similar architectural forms but can vary significantly in size and productivity, both within and across species (Duarte 1991). In a review of *Z. marina* worldwide, Olesen and Sand-Jensen (1994) found that above-ground biomass reached similar maximum amounts per area (median value 245 gDW m⁻²) regardless of shoot density (which was quite variable from 150 to 2,500 shoots m⁻²). Thus, within a single species, the same biomass could be achieved by small, high-density shoots or large, low-density shoots, indicating that *Z. marina* conforms to constant leaf biomass per unit area. However, this relationship has not been examined for other species, and comparisons among different species are uncommon (except see Duarte 1991). In Korea, where both *Z. japonica* and *Z. marina* are native, total biomass per area was similar, but above- and below-ground allocation differed (Lee et al. 2006), and maximum above-ground biomass for both species was in the lower range of those compiled by Olesen and Sand-Jensen (1994). Nevertheless, an invasive species might achieve higher maximum biomass than its native congener. So, one of our objectives was to compare biomass-density relationships for the two species throughout the year.

Two logical predictions can be made about how the presence of a congeneric species influences invasion success: A similar, new species might be able to invade easily, because it is “pre-adapted” to local conditions at the invaded site. Alternatively, its success might be reduced due to competition with, or natural enemies acquired from, the native species (Darwin’s naturalization hypothesis; Daehler 2001; Mitchell et al. 2006). These contrasting predictions have been tested by examining patterns of invasion success. Evidence is currently mixed about whether taxonomic similarity to a native species makes invasion more or less likely or has no effect (Duncan and Williams 2002; Ricciardi and Mottiar 2006). Interestingly, although *Z. marina* and *Z. japonica* are taxonomically related, published research suggests several life history and morphological differences between the two species. *Z. japonica* has been reported to invade higher intertidal elevations,

whereas *Z. marina* tends to occur below mean lower low water (MLLW) (Harrison 1982a, b; Thom 1990; Bulthuis 1995; Hahn 2003). Thus, *Z. japonica* occupies a more extreme environment, with greater fluctuations in temperature and desiccation stress due to more frequent exposure at low tide, for longer periods of time. This higher intertidal distribution could require a more “weedy” phenology or a more stress-adapted morphology (Duarte 1991). Indeed, *Z. japonica* in part of its introduced range has been reported to grow better under higher temperatures (Shafer et al. 2007; 2008) and to be essentially an annual, with almost all new shoots arising from seeds in spring (Harrison 1982b; Harrison and Bigley 1982). In contrast, many reports of *Z. marina* indicate it to be physiologically limited to the lower intertidal (Thom et al. 2003, Moore and Short 2006) with severe bottlenecks in recruitment (Orth et al. 2006b; Wisehart et al. 2007). These ideas point to the importance of making ecological, not just taxonomic comparisons to distinguish pre-adaptation and Darwin’s naturalization hypothesis, so our second objective was to examine seasonal variation in growth and reproduction.

Zostera marina shows substantial variation in morphology and reproduction as a function of depth and sediment type; for instance, subtidal populations in organic-rich sediments often consist of large shoots, whereas intertidal individuals in sandy substrates are often small with a high investment in sexual reproduction (Phillips et al. 1983; Baden and Bostrom 2001; Moore and Short 2006; Yoon 2006). *Z. japonica* has also been reported to have several morphotypes, for instance forming patches intertidally or interspersed with other seagrasses subtidally in southern Japan (Kuo et al. 2006). We carried out our study at multiple sites to account in part for within-species variation due to environmental conditions, making it easier to determine which characteristics consistently varied between the two species.

In this study we compared the distribution and life history traits of a native and non-native eelgrass species in an estuary where both are anecdotally believed to be thriving. As of 1997, *Z. marina* occupied 9.6% and *Z. japonica* 7.7% of Willapa Bay’s total area (35,700 ha) (Ruesink et al. 2006). At three sites along the estuarine gradient, we determined intertidal distribution, biomass-density relationships, and seasonal patterns of growth and reproduction.

Finally, we compiled all available records of density of the two species in Willapa Bay to assess long-term trends for evidence of invasion of *Z. japonica* to the detriment (or facilitation) of the native eelgrass.

Methods

Study sites

Willapa Bay is a macrotidal estuary on the outer coast of Washington state, USA. At 40 km long (N/S) and 10 km wide, it is the second-largest coastal estuary on the USA west coast. The bay contains extensive intertidal flats, with about half of the bay’s area exposed on extreme low tides (mean tidal amplitude = 1.9 m; Hickey and Banas 2003). *Zostera marina* is reported to occur below 0 MLLW (Thom et al. 2003), and the tideflats were historically unvegetated between the native eelgrass and marsh (above mean high water, ~ 3.2 m; Borde et al. 2003). These tideflats have been modified by a suite of prominent introduced species (Ruesink et al. 2006) and continue to be shaped by on-bottom oyster and clam aquaculture, which occur on about 20% of the intertidal area (Feldman et al. 2000). We focused on 3 sites arrayed from the mouth of Willapa Bay to about halfway along the estuary gradient on the western shore: Stackpole (ST: N46.5945, W124.0280), Oysterville (OY: N46.549, W124.013), and Nahcotta (NA: N46.4955, W124.029) (see figure in Ruesink et al. 2003). Water temperatures were recorded hourly by a temperature logger maintained by the Washington Department of Fish and Wildlife at the Port of Peninsula, which is within 0.5 km of our up-estuary site (NA), and at a permanent meteorological station at Toke Point, near the estuary mouth (<http://tidesandcurrents.noaa.gov>).

Distribution

At each site, we sampled eelgrass along three transects perpendicular to shore from the *Z. marina* zone to the upper limit of *Z. japonica* in July 2007. Actual tidal elevations were calculated from the amount of time that 2–3 points along the transect were uncovered at low tide, based on air and water temperatures logged at 12 minute intervals from 8 to

25 July 2005 (iButtons, Dallas Semiconductor; method in Ruesink et al. 2003). Because each tideflat had a different slope, the transects were different lengths (ST = 120 m, OY = 1,700 m, NA = 525 m), and we selected intervals to sample that generated 20–30 quadrat locations along each transect. Quadrats were 50 × 50 cm, inside which we measured % cover of *Z. marina* and *Z. japonica*, counted *Z. marina* shoots (distinguishing vegetative and flowering), subsampled *Z. japonica* shoots in a circle (diameter = 10 cm) at the center of the quadrat, and selected the shoot of each species that was closest to the center to measure shoot length. We collected 5 sediment samples (5 cm dia, 2 cm deep) along each transect. Sediments were dried and ashed (3 hr at 500°C) to determine organic content and were sieved (Ro-Tap) through 63 µm mesh to determine silt:sand ratio.

Morphology

Zostera marina was sampled 5 times (except missing initial sample at ST) and *Z. japonica* 10 times throughout 2004. For *Z. marina*, we collected above- and below-ground material by hand from 10 50 × 50 cm quadrats at each site. Shoots were distinguished as main, branch (originated within 5 internodes), flowering, or new recruit. Each vegetative shoot was measured from the first node to the end of the longest leaf (cm). Within each quadrat, above- (leaves, sheaths, spathes) and below-ground (rhizomes, roots) material was divided, dried (60°C to constant weight), and weighed (mg).

To sample *Z. japonica*, we collected sediment cores (10 cm diameter, 8 cm deep) and sieved them through 1 mm mesh. Six samples were taken at a lower elevation (close to but not within *Z. marina*) and 6 at a higher elevation within the *Z. japonica* zone at each site. Shoots were distinguished as vegetative, flowering, or new recruit. Each was measured for shoot length. Within each sample, above- and below-ground material was divided, dried (60°C to constant weight), and weighed (mg). We did not begin to track branching until Sept. 2004, but we collected additional samples (5 cores low, 5 cores high at each site) in June 2005 in which we also distinguished main shoots from branches (originated within 5 internodes).

Growth

Leaf growth rates were measured 5 times in 2004 for each eelgrass species. *Z. marina*: February, May, June, August, November; *Z. japonica*: March, May, July, September, December. For *Z. marina*, we measured 10 sets of 3–5 shoots for growth at each site, based on a modified leaf-marking technique (Zieman 1974; Ibarra-Obando and Boudouresque 1994). Shoots were marked at the leaf sheath with two small holes created by a hypodermic needle and then collected after three days. We measured only growing leaves (those that had marks that had moved at least 5 mm away from the basal meristem), dividing them into old (from the mark to the leaf tip) and new (from the mark to the leaf sheath where originally marked) material. These old and new portions were measured for length on a per-leaf basis and for dry biomass (60°C to constant weight, mg) on a per-shoot basis. We calculated raw shoot growth (new biomass per shoot per day) and relative growth rate (RGR, new biomass per old biomass, including only growing leaves).

For *Z. japonica*, we sampled growth in 5 lower and 5 higher plots at each site, using the clip and re-harvest method because shoots were too narrow to mark (Kaldy 2006). We embedded PVC rings (10 cm diameter, 8 cm depth) flush with the sediment to isolate and identify shoots. These shoots were clipped above the meristem. Generally 2 weeks later we returned to collect shoots, which we counted, measured 5 for maximum leaf length, and once again clipped biomass above the meristem to dry (60°C to constant weight) and weigh (0.1 mg). Based on results from other seagrasses, leaf-clipping underestimates production by about 50% (Kowalski et al. 2001).

Interannual variation in eelgrass abundance

We compiled data collected from eelgrass beds in Willapa Bay where summer (June–August) density measurements were available over at least 2 years. Among the cases included in the analyses, quadrat size varied (0.25–4 m²), and sample size was at least 10 replicates. In 2006–2007, we resampled areas of published density reports (Thom et al. 2003; Tallis et al. 2009), all three of our study sites from 2004,

and additional areas where we had unpublished data from previous years.

Statistical analyses

We did not perform a statistical analysis of intertidal distribution, but instead simply examined the extent of overlap between the native and introduced eelgrass. Shoot size for each species was analyzed separately as a function of tidal elevation by regression.

Species comparison

At each site, we sampled *Z. marina* near the upper limit of its contiguous distribution, *Z. japonica* near the lower limit of its contiguous distribution, which was close to *Z. marina* (“low” samples), and *Z. japonica* near the upper limit of its distribution (“high” samples). We considered these samples to have come from three “treatments” in analysis of variance (or non-parametric Kruskal–Wallis test when variance was unequal), blocked by site. Because sites were arrayed along the estuarine gradient, we considered site to be a fixed factor. In comparing species, we focused on two dependent variables related to reproductive effort and recruitment (maximum proportion of shoots flowering, and maximum proportion of shoots from seeds), and three related to biomass-density comparisons (maximum above-ground biomass, accompanying shoot density, and coefficient of variation of biomass throughout 2004).

Seasonal and spatial variation

Although *Z. marina* and *Z. japonica* were sampled at the same three sites, the timing and number of samples differed in 2004, making direct comparisons of the two species impossible across time. Instead, we examined how well morphological and life history traits were predicted by two seasonal indicators, daylength and water temperature. In ANOVA for *Z. marina*, site was a fixed effect, and daylength and water temperature were included as covariates. For *Z. japonica*, elevation (high, low) and a site \times elevation interaction were included as additional fixed factors. Dependent variables were: shoot density,

shoot length, above-ground biomass, below-ground biomass, proportion branching (*Z. marina* only), proportion flowering, raw shoot growth, and relative growth rate (*Z. marina* only). Variables were transformed when necessary to meet assumptions of normality.

Interannual variation

To determine overall changes in eelgrass in Willapa Bay, we performed a meta-analysis across all sites where eelgrass was sampled over multiple years. We standardized our data across sites by calculating the effect size, indicating how much eelgrass changed between the initial and final samples at a site, based on a common metric, Hedge’s *d* (Hedges and Olkin 1985). Positive *d* values indicate an increase in abundance over time, negative values indicate declines, and zero no change. Then, for each *Zostera* species, we calculated an average and confidence limit for effect size with Metawin 2.0 (Rosenberg et al. 2000), which weights effect sizes based on the inverse of variance.

Results

Distribution of native and non-native eelgrass

Although *Zostera marina* was previously reported in meadows between 0 and -1 m MLLW in Willapa Bay (Thom et al. 2003), it occurred up to $+0.6$ m MLLW in our transects, as well as in depressions at still higher elevations (Fig. 1a, c, e). The upper limit of *Z. japonica* reached at least $+1.5$ m MLLW, and it may have been able to occur still higher, but we ended our transects when we encountered marsh plants or banks. The lower limit of *Z. japonica* was difficult to define, as we occasionally saw it below MLLW, but it never became abundant underneath dense *Z. marina*. We observed substantial zones of overlap at two sites (ST, OY) between about 0.2 and 0.6 m MLLW, but this zone was mostly devoid of vegetation at the third site (NA). Shoot size varied substantially with tidal elevation in both species: lower plants had longer average lengths than did those at higher elevations, except for *Z. japonica* at OY, where the largest plants were in a depression holding water in the middle of the zone (Fig. 1b, d, f).

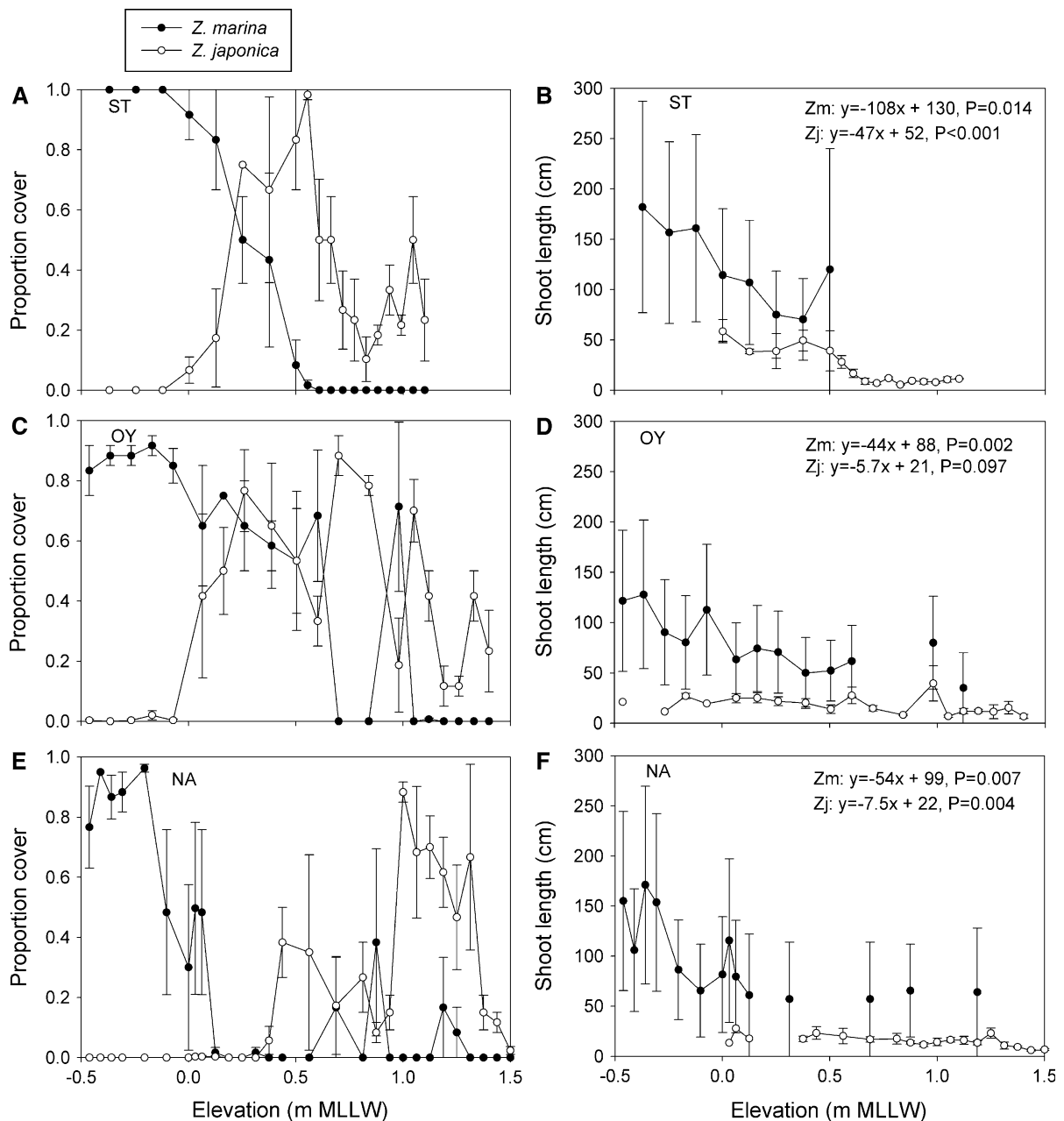


Fig. 1 *Zostera marina* and *Z. japonica* intertidal distribution at three sites in Willapa Bay, Washington. **a, c, e** Proportion cover; **b, d, f** Shoot length. Horizontal axis assumes constant slope interpolated and extrapolated from 2–3 points of known

tidal elevation. Error bars standard error of three replicates. *Inset* shows regression equation and *P*-value for length by elevation for each species at each site

Z. marina shoots (average 123, 78, 94 cm at ST, OY, NA) were five times longer than *Z. japonica* (average 22, 18, 16 cm).

Sediment samples collected along the transects reflected an estuarine gradient in sediment type and

also some variation from high to low elevation (Fig. 2a, b). NA, farthest from the mouth of the bay, had sediments with higher organic content and smaller grain size than at OY and, in the zone of *Z. japonica*, at ST. However, lower-elevation sediments

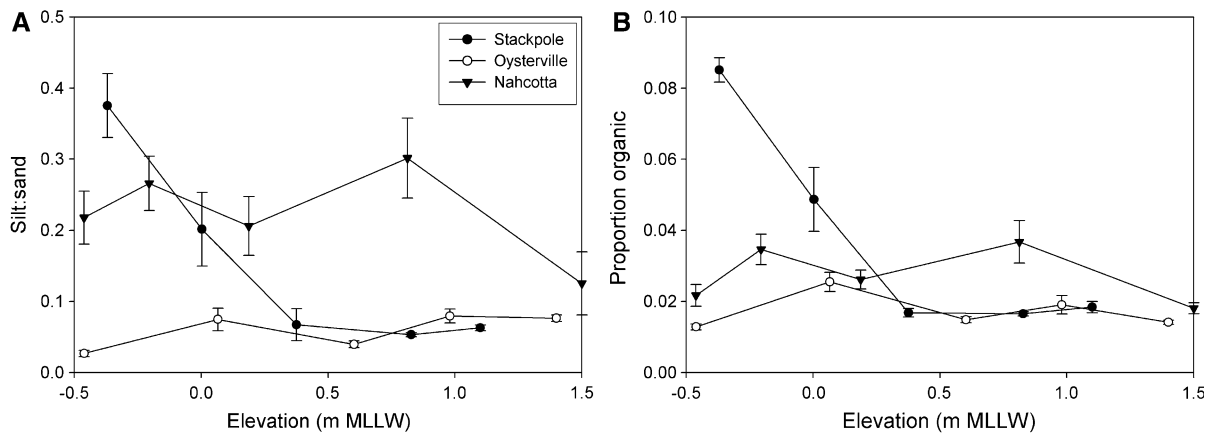


Fig. 2 **a** Silt:sand ratio and **b** proportion organic in sediment across tidal elevations at each site. Error bars, standard error of three replicates

at ST were also relatively silty in a depositional environment along a tideflat channel. (This was not the exact position of 2004 seasonal study.) There was no obvious difference in sediment type associated with the two *Zostera* species, and both occupied sediments with silt:sand ratios of 0.05–0.3 and 1–4% organic content (Fig. 2).

Species comparisons—reproduction and recruitment

Asexual reproduction contributed to a doubling in shoot density of *Z. marina* in February, when 50–60% of shoots were recent branches (<5 internodes since branching) (Fig. 3a). Recruitment from seed happened slightly later, peaking in May, and contributed a much smaller fraction of shoots (Fig. 3e). Additional samples from OY confirm this pattern, since no recruits were observed in March, and the proportion of new recruits remained high in early June (unpublished data). Flowering, which produced seeds for the following year, was most common in May and June (1–7%), although some still occurred in September (Fig. 3c). For *Z. japonica*, we had incomplete data on branching, but it appeared high during mid-summer when new branches in *Z. marina* were becoming less common: June samples for *Z. japonica* showed 60–90% of shoots were new branches (Fig. 3b). Recruitment from seeds peaked in March (up to 57%) but was evident until June (Fig. 3f). Flowering began in June and continued through October, with maximum levels of 13–34% of the population (Fig. 3d). Statistically, investment in

reproduction (maximum proportion flowering shoots) was larger in *Z. japonica* than *Z. marina* (Table 1), especially since *Z. japonica* flowered over a longer period. Recruitment showed higher mean values in *Z. japonica* than *Z. marina* (by an order of magnitude), but was also extremely variable among sites.

Species comparison—biomass-density patterns

Maximum above-ground biomass was slightly higher for *Z. marina* than for *Z. japonica* at either elevation (Table 1). However, all values were substantially lower than even the median values of leaf biomass per area compiled by Olesen and Sand-Jensen (1994): 245 vs. <143 gDW m⁻² in our study. At the lower part of its intertidal distribution, *Z. japonica* showed a higher coefficient of variation than in *Z. marina*, indicating more seasonal variation in above-ground biomass. The shoot densities achieved at these times of maximum biomass ranged from 69 to 353 m⁻² for *Z. marina* and exceeded 3,800 m⁻² for *Z. japonica* (Table 1).

Seasonal and spatial variation

In Willapa Bay, water temperatures lag daylength by about two months (Fig. 4), thus these covariates help distinguish between eelgrass phenology associated with mid-summer (daylength) versus late-summer (temperature). In *Z. marina*, both above and below-ground biomass were most strongly related to daylength, whereas significant relations to temperature in

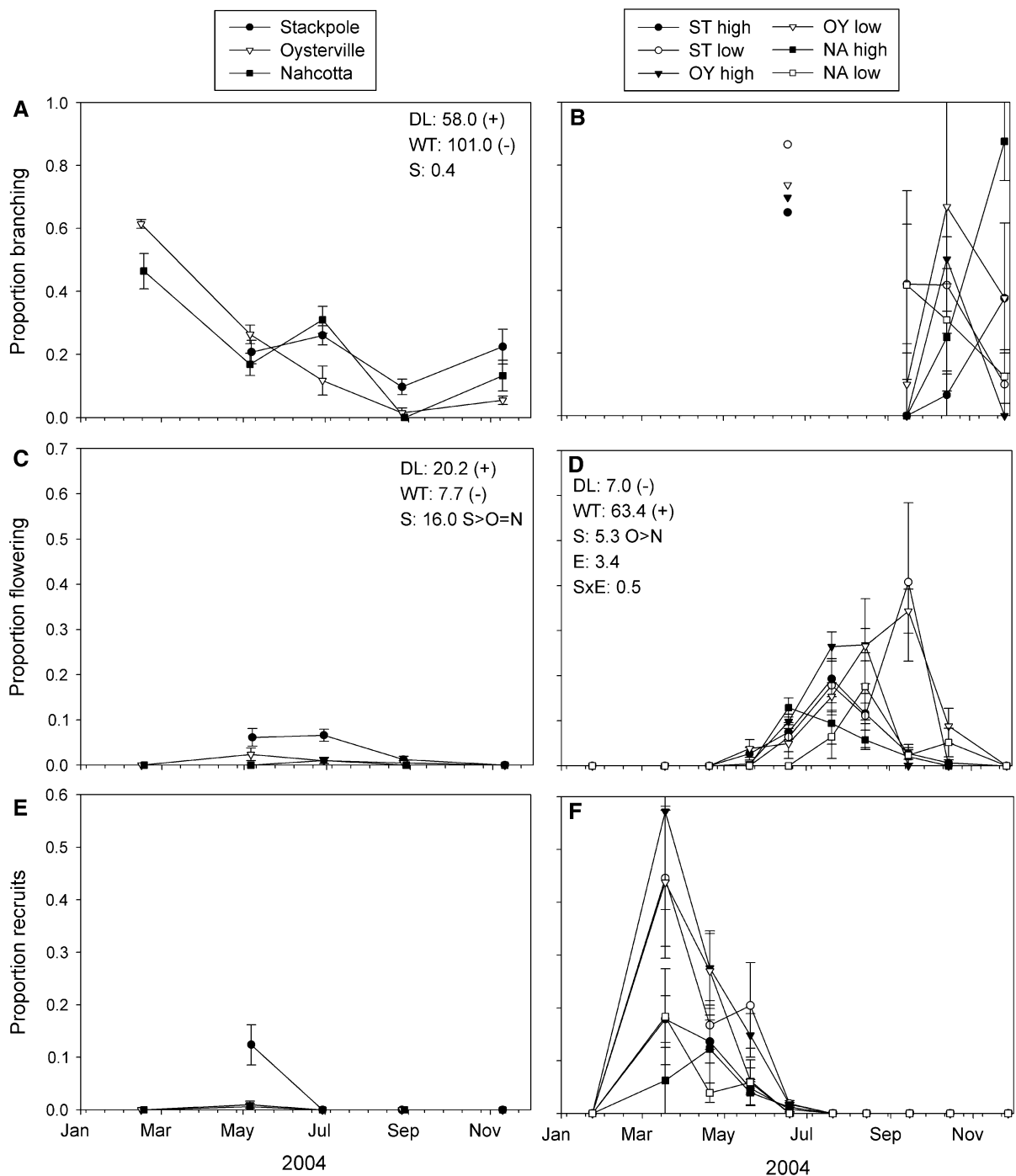


Fig. 3 Life history traits of *Zostera* spp. in 2004: **a, b** proportion branching, **c, d** proportion flowering, **e, f** proportion new recruits (seedlings). Scales are the same for *Z. marina* (on left) and *Z. japonica* (on right). Error bars standard error of 10 (*Z. marina*) or 5–6 (*Z. japonica*) samples. Inset shows *F*-values for ANOVA with predictor variables of daylength (DL), water

temperature (WT), site (S), elevation (E), and site × elevation interaction (S × E). (+) and (–) indicate the direction of relationship with significant covariates. >: significantly different in post-hoc analysis, Tukey's test. S—Stackpole, O—Oysterville, N—Nahcotta; hi—*Z. japonica* above 1 m MLLW, lo—*Z. japonica* near 0.5 m MLLW

Table 1 Direct comparison of life history traits of *Z. marina* (Zm) and *Z. japonica* (near its upper [Zjhi] and lower [Zjlo] elevation), showing site averages and results of analysis of variance

Trait	<i>Z. marina</i>	<i>Z. japonica</i> low	<i>Z. japonica</i> high	Blocked ANOVA or non-parametric Kruskal–Wallis
Tidal elevation where sampled	ST: 0.6 m OY: 0.5 m NA: <0.4 m	0.5 m 0.7 m 0.4 m	1.1 m 1.4 m 1.5 m	No analysis performed
Maximum prop. flowering shoots [Month]	0.07 [Jun] 0.02 [May] 0.01 [Jun]	0.18 [Jul] 0.34 [Sep] 0.18 [Aug]	0.19 [Jul] 0.27 [Aug] 0.13 [Jun]	Ln-trans $F_{2,4} = 14.9$, $P = 0.01$ Zjlo=Zjhi>Zm
Maximum prop. shoots from seeds [Month]	0.12 [May] 0.01 [May] 0.01 [May]	0.45 [Mar] 0.44 [Mar] 0.18 [Mar]	0.18 [Mar] 0.57 [Mar] 0.12 [Apr]	Ln-trans $F_{2,4} = 7.66$, $P = 0.04$ Zjlo≥Zjhi≥Zm
Maximum above-ground biomass (gDW/m ²) [Month]	130 (13.9) [Jun] 143 (14.1) [May] 85 (9.5) [Aug]	115 (46.3) [Sep] 87 (7.3) [Aug] 57 (19.6) [Aug]	84 (10.8) [Jul] 73 (11.6) [Jun] 69 (21.0) [Jul]	Kruskal–Wallis: Chi square = 5.96, $P = 0.05$, Zm > Zjlo = Zjhi
CV of above-ground biomass	0.33 0.51 0.59	1.00 1.03 1.00	0.66 1.24 0.74	$F_{2,4} = 7.2$, $P = 0.05$ Zjlo≥Zjhi≥Zm
Shoot density at maximum biomass (m ⁻²)	353 (39) 290 (14) 69 (7)	8264 (1496) 7360 (904) 3803 (1281)	7792 (875) 8388 (329) 5777 (388)	Ln-trans $F_{2,4} = 97.2$, $P = 0.0004$ Zjhi=Zjlo>Zm

Average values at each site were considered samples, and analyses were blocked by site. However, standard errors (SE) are presented when possible to indicate within-site variation among replicates. The blocking factor (site) was not significant (NS) in any analysis. > , significantly different in post-hoc analysis, Tukey's test

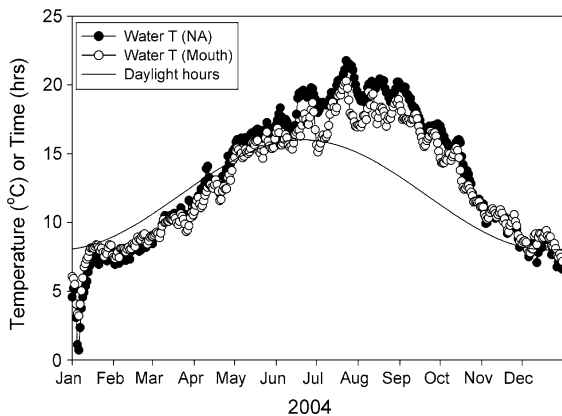


Fig. 4 Seasonality of daylength and water temperature in Willapa Bay, Washington. Mean daily temperature recorded at Port of Peninsula (near Nahcotta site) and at Toke Point (near mouth of Willapa Bay)

Z. japonica suggest a late-summer peak and low biomass through late-winter (Fig. 5c–f). *Z. marina* shoot density was correlated with daylength but shoot

length with temperature (Fig. 5a, g), as larger shoots dominated the population in late-summer when branching slowed (Fig. 3a, e). In *Z. japonica*, both density and length were positively correlated with daylength and temperature (Fig. 5b, h).

Sexual reproduction (flowering) in *Z. marina* was early (correlated with daylength) relative to *Z. japonica*, which had sexual reproduction correlated with temperature (Fig. 3c, d). Asexual reproduction (branching) was strongly inversely related to temperature in *Z. marina*, because rhizomes tended to branch in late winter and early spring (Fig. 3a).

Raw shoot growth in both species was correlated with daylength and temperature, indicating a broad summer peak (Fig. 6a, b). On a per-shoot basis, *Z. marina* growth was 100× faster than *Z. japonica*, but this essentially reflects their relative biomass (*Z. marina* 0.37–1.26 g/shoot in June vs. *Z. japonica* 0.01–0.013 g/shoot). Relative growth rates for *Z. marina* showed no variation across sites and were strictly a function of daylength, about 3× faster in

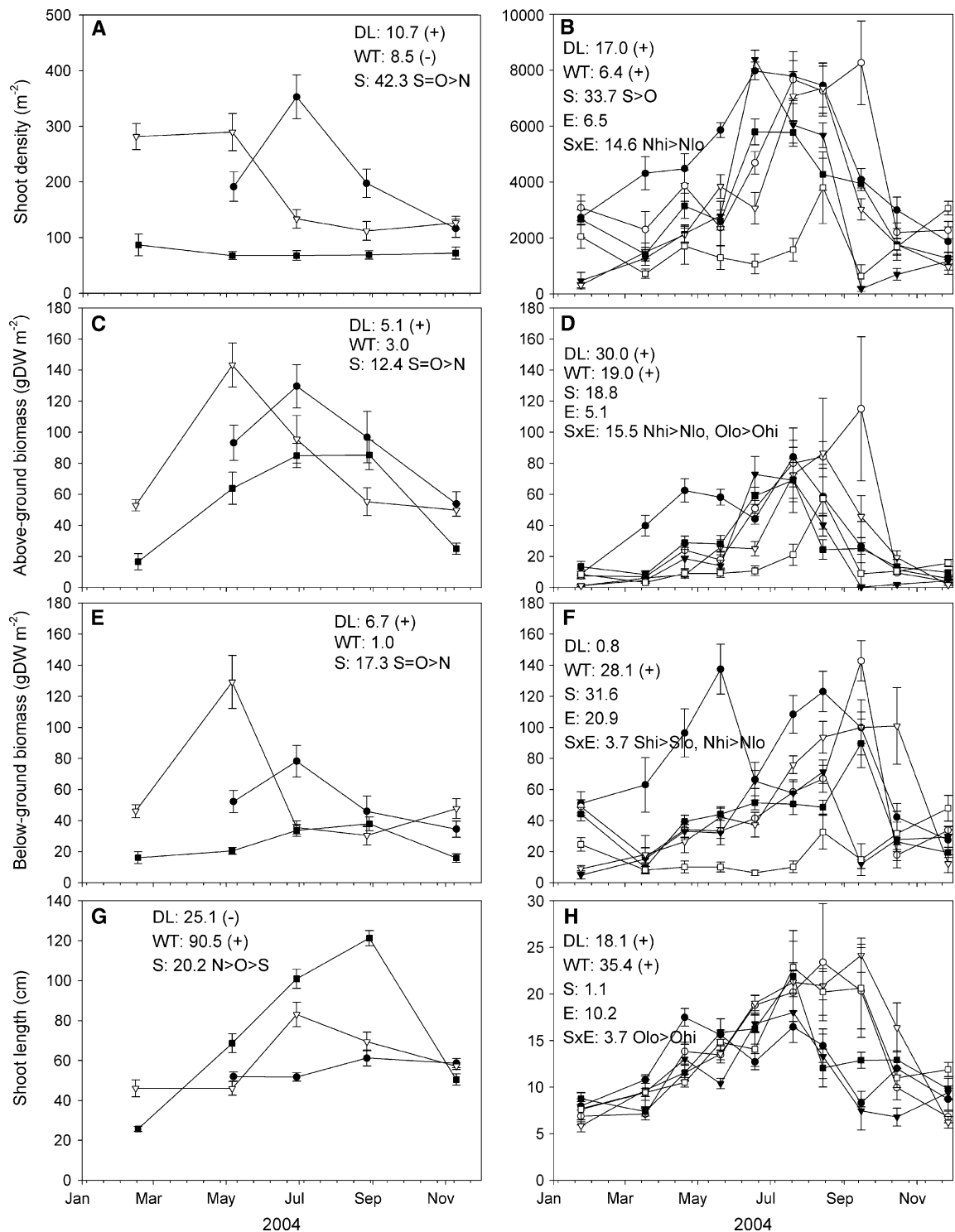


Fig. 5 Morphology and density of *Zostera marina* (on left) and *Zostera japonica* (on right). Y-axis scales are different. Symbols as in Fig. 3. Error bars standard error of 10 (*Z. marina*) or 6 (*Z. japonica*) samples. Inset shows ANOVA

results as described in Fig. 3. Shoot density, above- and below-ground biomass, and (for *Z. japonica*) shoot length required ln-transformation prior to analysis

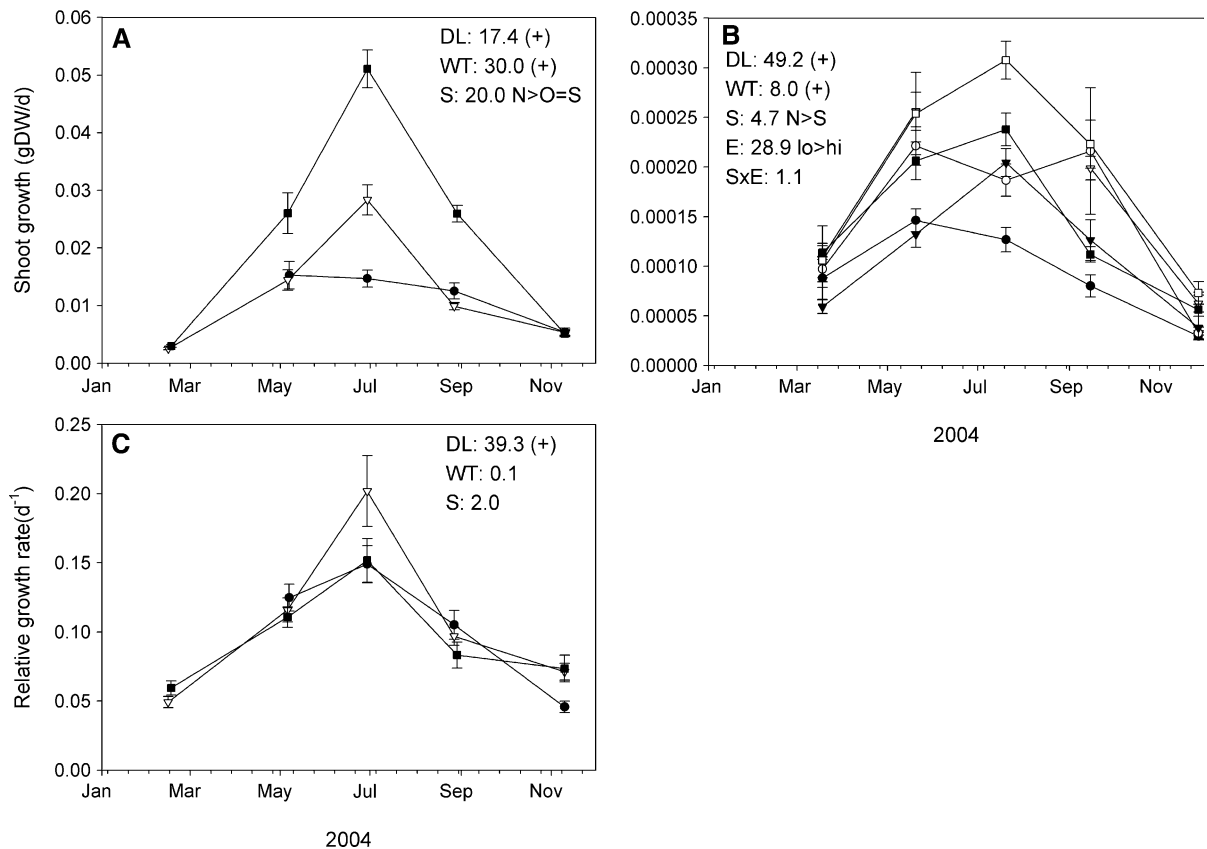


Fig. 6 Seasonal shoot growth of *Zostera marina* (on left) and *Zostera japonica* (on right). Symbols as in Fig. 3. Error bars standard error of 10 (*Z. marina*) or 5 (*Z. japonica*) samples.

summer than winter (Fig. 6c). After mid-summer, RGR declined, but because plants were on average larger, raw shoot growth remained high.

Interannual variation in eelgrass abundance

The time series we compiled (Tables 2, 3) confirmed anecdotal reports of substantial increases in eelgrass in Willapa Bay over the past decade. These increases have been particularly dramatic on wide tideflats that were historically unvegetated. From 2004 to 2007, the upper limit of continuous *Z. marina* at our Oysterville site (N46.54893 W124.01675) expanded horizontally 30 m up slope. From 2006 to 2007, the northern boundary of a *Z. marina* bed near our Stackpole site (N46.61473, W124.0318) expanded by 20 m towards an area of burrowing shrimp (*Neotrypaea californiensis*). For the 14 time series we compiled for *Z. marina*, ranging in length from 2 to 10 years,

Inset shows ANOVA results as described in Fig. 3. Shoot growth required ln-transformation prior to analysis

meta-analysis demonstrated an overall increase: d averaged 0.81 (95% confidence interval = 0.64–0.99). The results were significantly heterogeneous ($Q_{\text{total}} = 103.9$), and part of this heterogeneity was due to more dramatic increases at higher intertidal elevations (Table 2). In contrast, the 5 times series available for *Z. japonica* showed no overall change ($d = -0.48$, 95% CI = -1.11 – 0.14) (Table 3). Although *Z. japonica* densities were consistent between 2004 and 2007 at our study sites, the species has certainly increased in the 5 decades since its introduction.

Discussion

The invasion of *Z. japonica* on northeast Pacific tideflats provides an exceptional opportunity to study aspects of its phenology that determine its success,

Table 2 Summer (June–August) abundance of *Z. marina* over multiple years at particular locations in Willapa Bay

Site	Lat	Long	Elev (m MLLW)	Date	Density m ⁻² or cover %	SE [N]	Source
PNCERS Nemah Spit	46.5642	123.9583	−0.56	1998	43.3	15.8 [20]	1
					61%	15.5 [20]	
			−0.46	1999	60.1	30 [20]	1
					59.5%	27 [20]	
				2000	114.9	23.2 [20]	1
	46.5649	123.9573			63%	16.3 [20]	
				2001	62.7	25.5 [20]	1
					55.5%	22.6 [20]	
				2006	98.8	45.29 [20]	2
					60.5%	27.6 [20]	
PNCERS NW Long Island	46.5076	123.0064	−0.43	1998	57.1	16.5 [20]	1
					76.8%	13.8 [20]	
			−0.43	1999	64.8	29.4 [20]	1
					62.3%	30.2 [20]	
				2000	81	48.2 [20]	1
	46.5075	124.0059			75.0%	34.1 [20]	
				2001	82.4	32.8 [20]	1
					83.9%	21.8 [20]	
				2006	87	40.37 [20]	2
					72.7%	32.0 [20]	
PNCERS Jensen Pt.	46.4715	124.0081	−0.39	1998	14.3	10.4 [20]	1
					30.9%	21.6 [20]	
			−0.48	1999	30.3	24.6 [20]	1
					44.5%	31.5 [20]	
				2000	68.3	28.1 [20]	1
	46.4718	124.0023			91.8%	21.8 [20]	
				2001	75.4	33.6 [20]	1
					95.8%	9.2 [20]	
				2006	65.4	29.37 [20]	2
					89.3%	16.1 [20]	
OY LL	46.5487	124.01496	+0.5	2002	29.0%	4.4 [56]	3
				2007	77.8%	4.3 [20]	4
Stackpole flats	46.61204	124.02798	+0.6	2006	0	0 [60]	5
				2007	22.8 m ⁻²	5.3 [44]	5
Stackpole outer	46.61174	124.02517	+0.6	2002	53.7%	6.5 [25]	5
				2007	96.5%	2.3 [30]	5
Nemah ctrl	46.54841	123.93487	0	2001	90.5%	1.9 [20]	3
				2002	73.2	2.8 [20]	3
				2003	76.3	2.8 [20]	3
				2007	83.4	4.9 [20]	6
Jensen ctrl	46.47022	124.00455	0	2001	93.5%	3.9 [20]	3
				2002	98.8	0.6 [20]	3
				2003	94.0	2.2 [20]	3
				2004	93.9	3.1 [20]	6
				2007	97.0	0.8 [20]	6

Table 2 continued

Site	Lat	Long	Elev (m MLLW)	Date	Density m ⁻² or cover %	SE [N]	Source
Middle S	46.48928	124.01808	0	2002	24.4%	5.2 [30]	3
				2007	73.7%	5.8 [39]	5
Stony Pt 1	46.6794	123.92145	+0.6	2002	48.7%	7.1 [31]	3
				2007	79.9%	5.4 [35]	5
Stony Pt 2	46.68455	123.92597	+0.3	2002	15.5%	4.8 [30]	3
				2007	19.8%	6.1 [30]	5
Stony Pt 3	46.6857	123.92095	+0.3	2002	45.6%	9.3 [22]	3
				2007	94.9%	1.2 [17]	5
Mill Ch	46.470595	124.020791	+0.3	2004	96.4 m ⁻²	7.8 [10]	7
				2007	83.5	10.7 [15]	5
Peterson	46.43764	124.00729	−0.2	2004	68.8 m ⁻²	11.6 [10]	7
				2007	148	9.4 [20]	5

1, Thom et al. 2003; 2, M. Helsing-Lewis, unpublished; 3, Tallis et al. 2009; 4, This study; 5, J. L. Ruesink, unpublished; 6, B. R. Dumbauld, unpublished; 7, E. Wagner, unpublished

Table 3 Summer (June–August) abundance of *Z. japonica* over multiple years at particular locations in Willapa Bay

Site	Lat	Long	Elev (m MLLW)	Date	Cover % or density m ⁻²	SE [N]	Source
Stackpole slough	46.59501	124.02853	0.8	2004	8,017	683 [9]	This study
				2007	1,590	275 [9]	This study
Oysterville flats	46.54923	124.01988	1.1	2004	8,895	505 [9]	This study
				2007	3,125	464 [9]	This study
Parcel A	46.49585	124.02938	1.0	2004	4,715	396 [9]	This study
				2007	3,152	767 [9]	This study
Mill Ch	46.470595	124.020791	+0.3	2004	5.4%	2.1 [10]	J. L. Ruesink, unpublished
				2007	25.6%	7.8 [15]	J. L. Ruesink, unpublished
Peterson	46.43764	124.00729	−0.2	2004	0.1%	0.1 [10]	J. L. Ruesink, unpublished
				2007	0.2%	0.1 [20]	J. L. Ruesink, unpublished

and compare this to *Z. marina*, a co-occurring native congener. We specifically tested four patterns: intertidal distribution, biomass-density, seasonal growth and reproduction, and abundance over several years. Much of our data support a more colonizing strategy for *Z. japonica* than *Z. marina*, including its occupation of higher, more variable tidal elevations (Fig. 1), and its higher seasonal variation in biomass, with increases driven by effective sexual reproduction (Table 1; Figs. 3, 5). At large scales in Willapa Bay, the congeneric invader coexists with native eelgrass, reflecting marked differences in morphological and life-history traits, which may ultimately control the species' productivity and distributional limits in the intertidal zone.

Our comparisons show that *Z. japonica* is smaller than *Z. marina* and generally occurs at higher intertidal elevations, consistent with many previous observations (Harrison 1982a; Thom 1990; Bulthuis 1995). Recent laboratory investigations have revealed that individual leaves of *Z. japonica* lose water faster than *Z. marina* and also show less photosynthetic recovery after being dried to low water contents (Shafer et al. 2007). Thus, desiccation clearly damages *Z. japonica*, and the mechanism enabling occupation of mid-intertidal habitats may instead involve small leaves in close proximity to damp sediment, holding water at low tide, and/or high turnover rates of leaves. These ideas are consistent with both the higher intertidal elevation of *Z. japonica* and the inverse

relationship between shoot size and tidal elevation for both eelgrass species (Fig. 1).

Despite its order-of-magnitude smaller shoot size, *Z. japonica* reached levels of maximum biomass within 30% of *Z. marina* (Table 1). The rapid increase in biomass of *Z. japonica* each spring, as indicated by its high coefficient of variation relative to *Z. marina*, was achieved by large investments in sexual reproduction, effective recruitment from seed, and apparently a long season of asexual branching (Fig. 3). The life history strategy of *Z. japonica* would not have been predicted from reports in its native range: The fraction of flowering shoots was <10% at 20°N (Lee 1997, Huong et al. 2003), and <20% at 34–37°N (Lee et al. 2005, 2006). Interestingly, Lee et al. (2006) actually found higher reproductive effort in *Z. marina* than *Z. japonica* where they are both native on the south Korean coast. In Willapa Bay, the pattern was opposite, certainly improving the ability of *Z. japonica* to colonize new areas. It would be interesting to know more about the life history traits of *Z. japonica* at higher latitudes in its native range, where environmental conditions would correspond more closely to Willapa Bay at 46.5°N. In fact, more appears to be known at these latitudes in the introduced than native range: Flowering rarely exceeded 10% in an Oregon coastal estuary (45°N; Kaldy 2006), in line with *Z. japonica*'s life history in its native range, but averaged ~25% in British Columbia (49°N; Harrison 1982b), more similar to our results. Although the biomass achieved by *Z. japonica* was lower relative to *Z. marina* in Willapa Bay and elsewhere (Olesen and Sand-Jensen 1994), both biomass and density were at the high end of reports of *Z. japonica* where native or introduced (compare to Table 6 in Kaldy 2006).

Our comparisons of biomass, density, size, growth, and reproduction to daylength and water temperature were designed primarily to evaluate differences in the seasonal timing of life history events of the two eelgrass species. This analysis showed a late-summer decline in density but increase in shoot size for *Z. marina* (compared to broad peaks in density and shoot size for *Z. japonica*) and later flowering for *Z. japonica* than *Z. marina* (Figs. 3, 5). Seagrasses often increase in productivity in spring and decline in fall, and temperature (rather than light) has been invoked as a mechanism for two reasons: biochemical reactions are temperature sensitive, whereas light

availability is strongly modified by factors other than daylength (Lee et al. 2007). Thus, it was initially counterintuitive that relative growth rate of *Z. marina* was correlated only with daylength, not water temperature (Fig. 6c). We suspect this may be due to the large changes in daylength at the latitude of Willapa Bay, nearly doubling from winter to summer, coupled with the fact that water temperatures stayed at 15–20°C for nearly 5 months in 2004 (mid-May to October). In a recent review, this temperature range emerged as optimal for *Z. marina* growth, as well as for *Z. japonica* (Lee et al. 2007). Shafer et al. (2008) came to a different conclusion about the temperature-dependence of eelgrass growth in the northeast Pacific based on two studies not included in the review, suggesting that optimal temperatures for *Z. japonica* (20° to as high as 30°C) were higher than for *Z. marina* (growth impaired above 15°C), and this could help explain their intertidal distribution. However, we found that the two eelgrass species had similar patterns of productivity (e.g. raw shoot growth, above-ground biomass) with respect to seasonality of temperature, although not in terms of the magnitude and seasonal timing of reproduction and survival (Figs. 3, 5). Our results for seasonality of production are consistent with Yaquina Bay, Oregon, where RGR of *Z. marina* is light-regulated (Kaldy and Lee 2007) and *Z. japonica* production responds to both temperature and light (RGR not available; Kaldy 2006).

Based on our data and others (Nomme and Harrison 1991a; Bando 2006; Shafer et al. 2007; Almasi and Eldridge 2008), it seems likely that *Z. japonica* thrives in the mid-intertidal zone of Willapa Bay because of its small size and high reproductive output, allowing it to spread quickly where abiotic conditions are variable and stressful, but competitive effects are low. Compared to introduced populations to the north and south, *Z. japonica* in Willapa Bay has the “best of both worlds”: high sexual reproduction and germination from seed as in annual plants in British Columbia (Harrison 1982b), and over-winter persistence and effective asexual reproduction as in Yaquina Bay, Oregon (Kaldy 2006).

At lower elevations in Willapa Bay, biological interactions appear strong. Unvegetated habitats can occur at suitable tidal elevations due to burrowing shrimp (Dumbauld and Wyllie-Echeverria 2003, Almasi and Eldridge 2008), and presence of shrimp in the unvegetated zone at NA may underlie the

disjunct distributions of eelgrass congeners there. When burrowing shrimp were removed from this particular zone by application of carbaryl, *Z. japonica* rapidly (albeit temporarily, due to the small-scale experiment) expanded its distribution below +0.55 m MLLW into the treated strips (Dumbauld 1994). The difference in overlap that we observed among three sites in Willapa Bay is just one instance of many population characteristics that varied among sites (see statistics provided in Figs. 3, 5, 6), without masking congeneric differences. Indeed, such spatial variation certainly extends to other parts of *Z. japonica*'s introduced range, for instance, extensive overlap with *Z. marina* at Padilla Bay, Washington (Hahn 2003) and Roberts Bank, British Columbia (Nomme and Harrison 1991b), but an unvegetated zone in Yaquina Bay, Oregon (Almasi and Eldridge 2008, B. Dumbauld, pers. obs.). In Willapa Bay, *Z. japonica* is also negatively affected by competition with *Z. marina* (Bando 2006). Although these experiments were carried out at +1–2 m MLLW, they provide a tentative explanation for sparse occurrences of *Z. japonica* within the *Z. marina* zone. Similarly, removal of *Z. marina* from a zone of congeneric overlap enabled more rapid population increase by *Z. japonica* (Nomme and Harrison 1991b).

The role of native eelgrass meadows in reducing the tidal range of *Z. japonica* remains to be worked out through experiments in the low intertidal zone. Regardless, the ability of *Z. japonica* to exploit higher elevations than *Z. marina* prevents the native congener from affecting its invasion there directly. Indirectly, effects through shared enemies are also expected to be weak, given low epiphyte loads on eelgrass in Willapa Bay (<3% of biomass; Thom et al. 2003) and infrequent herbivory from migrating waterfowl (Baldwin and Lovvorn 1994) or invertebrates (Thom et al. 1995; Keiser 2004). Thus, even if further studies ultimately provide experimental evidence of biotic resistance via competitive exclusion within the *Z. marina* zone (as in Darwin's naturalization hypothesis), *Z. japonica* can be considered to be pre-adapted to Willapa Bay's tideflats. However, this pre-adaptation may not simply reflect taxonomic similarity, but the fact that the two species naturally co-occur in the western Pacific (Lee et al. 2006), so *Z. japonica* has already exhibited an ability to use similar intertidal habitats. Additionally, *Z. japonica*'s extensive native range may reflect broad environmental

tolerances, for instance of seasonal and tidal variation, as shown in a congener comparison of >100 pairs of invasive and non-invasive terrestrial plants (Goodwin et al. 1999).

The life history of introduced *Z. japonica* in Willapa Bay should contribute to making it a particularly good colonizer, given its capacity to increase rapidly from low density through both sexual and asexual reproduction. Indeed, Bando (2006) found that areas cleared within a zone of overlap between the two eelgrass species disproportionately recovered to *Z. japonica* over 2 years. However, it seems unlikely that *Z. japonica*'s colonizing ability will lead to a replacement of the native by introduced eelgrass over time. Interannually, *Z. marina* has increased at multiple sites in Willapa Bay (Table 2). It may be the case that *Z. japonica* actually facilitates *Z. marina* at a landscape scale due to its ability to retain water and allow persistence of *Z. marina* at a higher elevational limit. Such a hypothesis that thick eelgrass holds water at low tide has been suggested previously (Thom 1990), and removal of *Z. japonica* (>100 m²) impairs its own growth (C. Tsai, J. Ruesink, A. Trimble, unpublished). Extending this benefit of congeneric neighbors to intertidal *Z. marina* seems plausible, although mechanisms for *Z. marina*'s expansion remain to be tested directly. Overall, from this congener comparison, we found little evidence for Darwin's naturalization hypothesis, but support for pre-adaptation and a colonizing life history of the introduced species. Facilitation has not previously been suggested in congener comparisons, but may be important if the invader engineers habitat such that the realized niche of the native species expands. Ultimately, the mechanisms behind changes in distribution and abundance will require manipulative experiments designed to understand how the two *Zostera* species interact across the physical gradients of the intertidal zone.

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